

# Habitat fragmentation has some impacts on aspects of ecosystem functioning in a sub-tropical seagrass bed



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## ABSTRACT

Habitat fragmentation impacts ecosystem functioning in many ways, including reducing the availability of suitable habitat for animals and altering resource dynamics. Fragmentation in seagrass ecosystems caused by propeller scarring is a major source of habitat loss, but little is known about how scars impact ecosystem functioning. Propeller scars were simulated in seagrass beds of Abaco, Bahamas, to explore potential impacts. To determine if plant-herbivore interactions were altered by fragmentation, amphipod grazers were excluded from half the experimental plots, and epiphyte biomass and community composition were compared between grazer control and exclusion plots. We found a shift from light limitation to phosphorus limitation at seagrass patch edges. Fragmentation did not impact top-down control on epiphyte biomass or community composition, despite reduced amphipod density in fragmented habitats. Seagrass and amphipod responses to propeller scarring suggest that severely scarred seagrass beds could be subject to changes in internal nutrient stores and amphipod distribution.

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## 1. Introduction

Habitat fragmentation is a process through which a continuous landscape is broken into smaller fragments or patches (Laurance et al., 2002; Feeley and Terborgh, 2008), often resulting in reduced areal coverage, higher proportion of edge habitat, and increased predation risk (Turner et al., 2001). In coastal marine ecosystems, habitat fragmentation can be a natural process driven by waves or currents (Fonseca et al., 1998), as well as by anthropogenic activities such as boat traffic, dredging, and eutrophication (Short et al., 2011). The rate of seagrass loss has accelerated in recent decades with global seagrass coverage reduced by one-third since 1879 (Waycott et al., 2009). These losses can be associated with substantial loss of ecosystem services (Waycott et al., 2009).

Edges caused by fragmentation are dynamic regions characterized by variable microclimates with temperatures, water/airflow, and habitat complexity different from habitat interiors (Turner

et al., 2001; Bologna and Heck, 2002; Ries and Sisk, 2004). This increased variability in edge habitats can affect the ecological relationships among organisms. For example, decreases in faunal abundances at the edge of seagrass patches are often attributed to increased predation (Irlandi, 1994; Bell et al., 2001; Peterson et al., 2001; Uhrin and Holmquist, 2003). Uhrin and Holmquist (2003) found crab and mollusk densities were lower up to 5 m away from recently-made scars in seagrass meadows (Uhrin and Holmquist, 2003). Conversely, some invertebrate prey species, including gammaridean amphipods, are found at higher densities at edges (Bologna and Heck, 1999; Eggleston et al., 1999; Arponen and Boström, 2012). Amphipods are hypothesized to settle in these edge habitats because current flow is reduced by the aboveground structure of seagrass (Fonseca et al., 1982), providing a more amenable environment (Tanner, 2003).

Gammaridean amphipods are important grazers in seagrass systems, consuming macro- and micro-algae growing on the substrate or on seagrass leaves. Gammaridean amphipods have strong impacts on regulating epiphyte growth on seagrasses, and can reduce the impacts of epiphyte-induced shading of seagrasses even under eutrophic conditions (Orth and van Montfrans, 1984; Neckles et al., 1993; Hughes et al., 2004; Jaschinski and Sommer, 2008;

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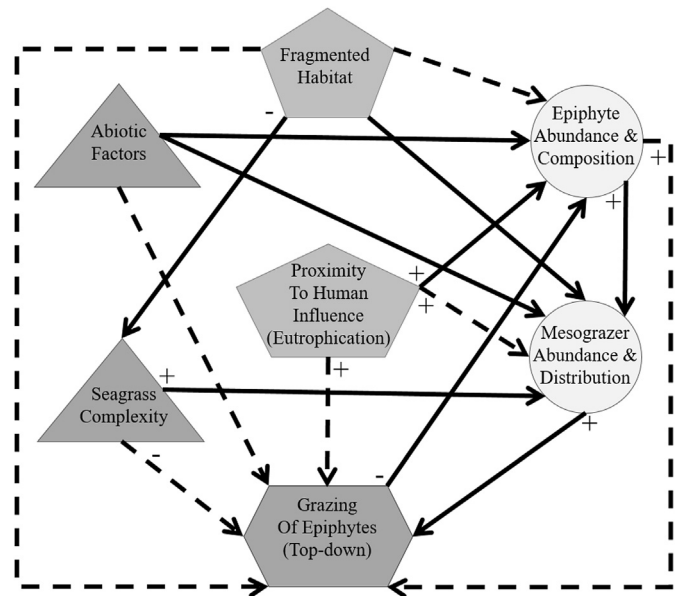
Spivak et al., 2009; Cook et al., 2011; Whalen et al., 2013; McSkimming et al., 2015). Species identity, richness, and diversity of amphipods mediates the top-down effect on seagrasses. A diverse amphipod community may efficiently reduce epiphytes belonging to different phototrophic groups because different amphipod species have different feeding preferences and abilities (Duffy and Harvilicz, 2001). As such, grazer diversity facilitates more complete use of epiphyte resources and (Duffy et al., 2001), depending on the composition of grazer species, can even increase seagrass biomass indirectly via epiphyte removal (Duffy et al., 2003). This also has implications for higher trophic levels, as amphipods are a major food source for many predatory fish and decapod species (Brook, 1977; Young and Young, 1978).

Few studies have investigated effects of fragmentation on amphipod communities in continuous seagrass beds. Most studies examining amphipod responses to fragmentation have instead been conducted using small, artificial, seagrass patches in unvegetated habitats adjacent to continuous seagrass beds (Healey and Hovel, 2004; Arponen and Boström, 2012; Pierri-Daunt and Tanaka, 2014). Understanding of amphipod responses to changes in patch size and level of isolation from the main seagrass patch was enhanced, but the studies did not focus on actual habitat fragmentation in natural systems (see Fahrig, 2003). The objective of our study was to examine if fragmentation caused by propeller scarring impacts the structure and function of seagrass ecosystems, as mediated by changes in resource availability and amphipod grazer communities (Fig. 1; Table 1). To test this, we simulated propeller scars in a seagrass bed on Abaco, The Bahamas. Additionally, we measured effects of grazers on epiphyte communities by removing grazers from half our experimental plots. We evaluated seagrass primary production (hypothesis 1 – see Table 1), nutrient and isotope values (hypotheses 2–3), epiphyte biomass and community structure (hypotheses 4–5), grazer abundance and community structure (hypotheses 6–7), and plant-grazer interactions (hypothesis 8).

## 2. Materials and methods

### 2.1. Site description and experimental design

The study was conducted at two sites in Abaco, The Bahamas (26°25'N, 77°10'W) from August to October 2014. The coastal areas of Abaco are primarily phosphorus-limited (Allgeier et al., 2010). Allochthonous nutrient input is localized in areas of high human populations around Abaco (Stoner et al., 2011), and can influence seagrass productivity and epiphyte community composition. One site, Cherokee Sound, was located closer to human influences than the other site, Jungle Creek. Both sites were characterized by depths of ~1.5 m at high tide with >50% *Thalassia testudinum* cover (Fig. 2). Forty experimental plots were established across a continuous seagrass landscape, and replicates of each treatment combination (n = 10) were randomly assigned (Fig. 3). Amphipod abundance and fragmentation treatments were manipulated over the course of 5 weeks at the two sites (site was one factor in the design). The factor of “grazing” consisted of two levels (amphipod exclusion and control). The factor of “fragmentation” also consisted of two levels (fragmented and continuous control). Edge and interior sampling plots were collected from the fragmented treatments only to test for edge effects (Table 2). Seagrass, amphipod, and epiphyte samples were collected within 15 cm of carbaryl blocks or control plot markers at continuous, interior, and edge locations at the end of the experiment.



**Fig. 1.** Conceptual diagram of hypothesized direct (solid lines) and indirect (dashed lines) interactions among abiotic factors, seagrass complexity, epiphyte abundance & composition, mesograzer abundance & composition, fragmented habitat, nutrient enrichment, and epiphyte grazing (top-down control). Interactions are designated as positive (+) or negative (-). No symbol indicates a change that is not determined to be either positive or negative. Pentagons are anthropogenic stressors (independent variables), the hexagon is a natural stressor (independent variable), circles are dependent variables, and triangles are independent variables.

### 2.2. Fragmentation treatment

Plots were chosen based on homogeneous cover of benthic vegetation (seagrasses and macroalgae) across a circular area 6.5 m in diameter, then were randomly assigned as a control or fragmented treatment. A simulated propeller scar was created around the circumference of the fragmented plots to a width of 25 cm (approximate width of propeller scars in the area) using hedge clippers. Circular plots were chosen so samples collected from plot interiors were equidistant from the scar in all directions. This scar design, while rare in shallow seagrass ecosystems, also allowed for us to test the effects of scarring and fragmentation, as would be seen in moderate-to severely-scarred seagrass beds, while controlling for the age of the scar, distance to patch edge, patch shape, and patch size. This configuration was chosen to simulate a moderately scarred seagrass bed, such as that found by the entrance or exit of a channel. Scars crisscross in these areas creating a patchy environment. Simulated scars in our study were used to simulate this patchy environment, but they also had to be sufficiently large to identify an edge effect, if any. To create the scars, seagrasses and macroalgae were removed at the sediment surface, and regrowth was trimmed weekly. Rhizomes were severed at the scar edge to prevent transfer of nutrients from adjacent short shoots. Actual propeller scars caused by motor boats often remove sediment and destroy the rhizosphere of seagrasses thereby increasing the time to full recovery of a scarred seagrass bed. As such, results from this experiment are conservative. All experimental plots had a diameter of 6.5 m (6 m internal diameter and 0.25 m propeller scar around the perimeter of fragmented plots, 6.5 m diameter for continuous plots) with an area of 33.2 m<sup>2</sup>. Plot centers were 10 m apart to ensure no cross-contamination by treatments with carbaryl (Fig. 3).

To test for fragmentation effects, samples were collected from the center of both fragmented and continuous plots. Samples were also collected from the edges and interior locations of a fragmented

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